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The Influence of Climate and Depositional Environment on the Distribution and Evolution of Pennsylvanian Coal-Swamp Plants

Introduction

Most evolutionary and ecological concepts of Late Carboniferous plants are based on fossils from wetland depositional environments of tropical Euramerica (Chaloner, 1958; Pfefferkorn, 1980). Although tropical wetlands and other lowland regions included a variety of habitats from floodplains to coal swamps, the sharpest ecological distinction was between peat-accumulating, coal-swamp environments and those with mineral-rich or clastic substrates. Coal-swamp environments were poor in nutrients, low in pH, poorly oxygenated, and under the strong influence of periodic standing fresh water. Plant remains preserved in coal balls as permineralized peat reflect the standing vegetation that formed the autochthonous or hypoautochthonous deposits and thus are less influenced by taphonomic factors than are compression assemblages. Clastic-substrate environments were usually more diverse floristically than were coal swamps and were edaphically much less uniform, although generally more nutrient-rich. Fossil plants preserved in these compression-impression assemblages were strongly influenced by taphonomic factors and yield considerably different morphological information than do anatomically preserved plants of coal-ball peats.

The kinds of factors that influenced the composition of plant communities in coal swamps include (1) expansion in abundance of previously uncommon plants present within the swamps; (2) migration into coal swamps of plants from clastic environments, which can be deduced from an understanding of ecology and the distribution of groups through time; (3) regional or general extinction, which is biostratigraphically obvious from numerous sources; and (4) evolution, which occurred both inside and outside the coal swamps. Evolutionary changes, recognized as speciation, are by far the most difficult to deduce and document in detail solely on the basis of evidence from coal swamps.

Coal palynology and coal balls indicate that the vegetation of Pennsylvanian coal swamps varied both stratigraphically (temporally) and regionally (spatially) in taxonomic composition and relative dominance of the constituent plants. During most of the Pennsylvanian, the vegetation in stratigraphically consecutive coal swamps tended to vary slightly. These periods of relatively little change were interrupted by geologically brief periods of major change that occurred approximately synchronously over a widespread geographic region. Evidence from coal resources, sedimentology, and paleogeography suggests that changes in vegetation were mediated by climate, particularly by available moisture (Zangerl and Richardson, 1963; Peppers, 1979; Broadhurst, Simpson, and Hardy, 1980; Phillips, Shepard, and DeMaris, 1980; Phillips and Peppers, 1984). The ecological amplitudes of the dominant trees in coal swamps (Phillips and DiMichele, 1981; DiMichele and Phillips, n.d.) support the patterns of climatic change deduced from other sources of evidence.

The major changes in coal-swamp vegetation occurred on a Euramerican-wide scale at the onset of and during two intervals that have been interpreted as having been drier. These dry intervals were progressively more severe and led to an even more severe third pulse at the beginning of the Permian (Phillips and Peppers, 1984). The synchronous change in vegetation of coal swamps over such different basinal settings as the Western Coal Region and the Appalachian Coal Region, and the occurrence of synchronous extinctions across Euramerica, imply further that climate was a controlling factor.

The Influence on Coal-Swamp Vegetation of Climate and Geologic Factors

The Euramerican coal belt occupied an equatorial position and had a tropical climate during Pennsylvanian time (Ziegler et al., 1981; Schopf, 1973, 1975, 1979). The numerous coals and thick accumulations of sediment in cratonic basins indicate that temperature and moisture availability combined with favorable tectonic settings to allow the development of lowland swamps, many of which were of great areal extent (Wanless, et al., 1963; Wanless, Baroffio, and Trescott, 1969). Large accumulations of peat resulted in bituminous coal seams up to four meters in thickness. Phillips, Shepard and DeMaris (1980) and Phillips and Peppers (1984) have plotted the stratigraphic distribution of identified coal resources in the United States. Patterns in the increase and decrease of these coal resources coincide broadly with the timing of continental collisions and mountain building that occurred during the Pennsylvanian (Ziegler et al., 1981; Parrish, 1982). Phillips and co-workers presume that the relative abundance of coal generally reflects the amount of total moisture available to the lowland regions in which coal swamps formed, assuming that otherwise favorable depositional conditions existed. We presume that most swamps formed in freshwater areas, although some coal-swamp plants may have been tolerant of brackish water. Independent studies of sedimentological patterns, where available, support these deductions (Zangerl and Richardson, 1963; Broadhurst, Simpson, and Hardy, 1980), at least as inferred for the first drier interval.

The flora and vegetation of these Pennsylvanian tropical coal swamps were strongly controlled by availability of fresh water during the Pennsylvanian and thus represent an index for the prevailing conditions of wetness during the existence of a swamp. Consequently, through geologic time, changes in coal-swamp vegetation reflected long-term climatic trends in wetness during the Pennsylvanian Period. Because of the water-holding capacity of the peat substrate, coal-swamp floras should have been less sensitive to minor fluctuations in moisture availability than were clastic-substrate floras (clastic swamps and other lowland vegetation). Therefore, the plant composition of the coal balls should reflect the regional climate. We would expect coal-ball floras to be more sensitive indicators of climatic trends than are compression floras because coal swamps were ecologically more homogeneous and had a distinct vegetation that accumulated *in situ*. Complicating the influence of climatic change were widespread tectonic events and eustatic sea-level fluctuations that affected directly the nature and extent of coastal regions available for swamp development, with the result that much of the change we see may have been a consequence of repeated major marine transgressions or regressions. However, once peat-forming swamp vegetation evolved, climatic fluctuations would be one of the most important causes of change in the composition of the swamps through direct or indirect influence on migrations, extinctions, and evolution.

The Pennsylvanian Period can be divided into five broad climatic intervals (fig. 8.1) based on patterns in coal resource abundance and

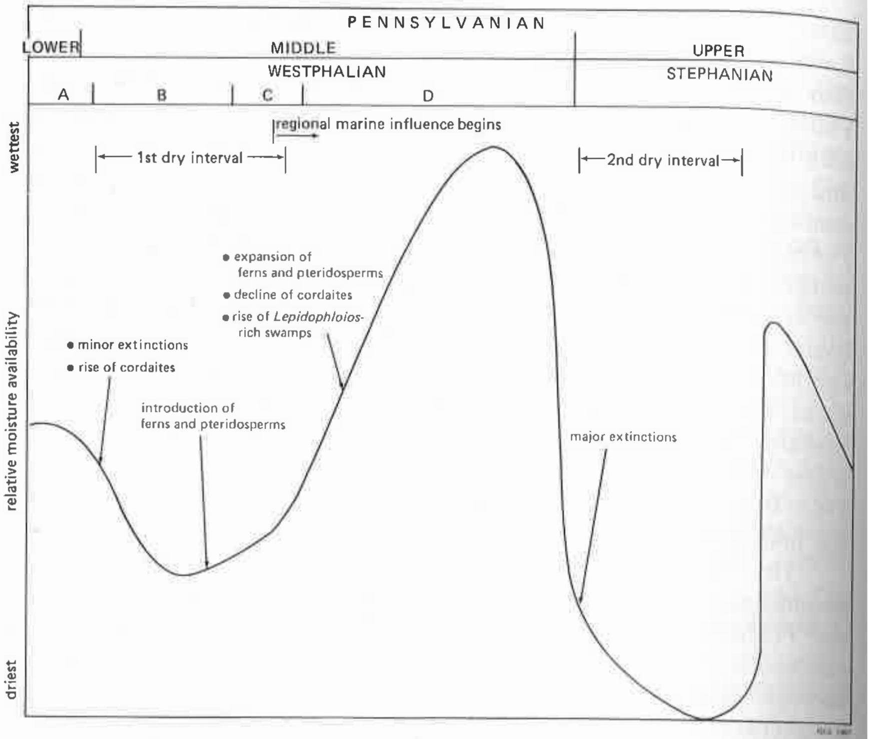

Fig. 8.1. Pattern of inferred moisture availability during the Pennsylvanian (after Phillips and Peppers, 1984).

corroborated by vegetational changes. (1) The Lower Pennsylvanian (Westphalian A) was a time of moderate, probably seasonal wetness. (2) During the early part of the Middle Pennsylvanian, a decline in general moisture availability began, apparently throughout most of Euramerica. This gradual decline was most severe during late Westphalian B time, after which a gradual increase in available moisture began. (3) This increase of moisture, perhaps a consequence of greatly reduced seasonality, culminated in the most favorable period for wetland vegetation during the late Middle Pennsylvanian (middle to late Westphalian D), at least in what is now the United States. During this increase in moisture, brackishness in coal swamps occurred in the Illinois Basin Coal Field due to widespread marine transgressions that began during the late Westphalian C and profoundly affected diversity by regionally masking the effects of available fresh water. (4) An apparently precipitous decline in availability of fresh water in mesic lowland areas and swamps occurred at the boundary between the

Middle and Upper Pennsylvanian (Westphalian D–Stephanian A) in the Midcontinent region of the United States. (5) A return of climatic or tectonic conditions favorable for accumulation of thick peat deposits occurred during the second half of the Upper Pennsylvanian and was terminated by the onset of drier conditions in the Permian.

The drier intervals appear to have been progressively more severe. This is suggested by the successively greater disruption of coal-swamp communities, the more widespread nature of extinctions, and the rise to dominance of species that were progressively better adapted to cope with moisture stress. Coal swamps of the wetter intervals were relatively extensive and were often sites of very thick peat accumulation. These swamps were dominated by lycopods during the Lower and Middle Pennsylvanian and by tree ferns during the Upper Pennsylvanian. Coal swamps of the drier intervals were of limited areal extent and of variable thickness. Coal balls from coals of drier intervals are composed of a high percentage of roots, thus implying decay of aerial plant litter. The kinds of plants that dominated these swamps varied, but gymnosperms, particularly cordaites in the Middle Pennsylvanian, and tree ferns became significant parts of the vegetation at the expense of lycopods.

During periods of low moisture, coal swamps shrunk in size, became more isolated, thus local and regional variability of the flora became more common. A peat substrate presents an edaphic barrier to the migration of clastic-substrate plants onto peat substrates. This, in effect, makes coal swamps "closed systems"; that is, the development of local and regional variability of coal-swamp floras would affect the plant composition of later coal swamps, which were most likely to be populated by plants with coal-swamp ancestries. The spatial compression of vegetation confined to contracting swamps may have altered ecological relationships among species, caused local extinctions, and disrupted the genetic continuity of more extensive populations. One would predict that, as a consequence of the difficulty that many small populations would have had in maintaining continuity, these drier intervals were the most favorable either for the introduction of species into coal swamps from environments outside coal swamps or for the evolution and establishment of new species derived from coal-swamp ancestors. Smaller, drier coal swamps would have had a greater margin-to-area ratio, providing for more "edge effects" — that is, the length of ecotones would be increased relative to the area of the swamps isolated from contact with clastic-substrate vegetation. Thus, new species could be introduced in areas where resources were made available by disruption of the existing vegetation. The appearance of forms from the clastic-substrate areas also may be expected if swamps were drier, generally or seasonally, because there would be more areas of decaying, exposed peat substrate. This is suggested by the higher root-shoot ratios in coal balls deposited during a dry interval.

Coal Swamps as Evolutionary Islands

Most of the evolutionary inferences concerning Pennsylvanian plants have come in recent years from studies of coal balls. Coal balls provide some of the best-preserved plant material in the entire fossil record and morphological and anatomical information rivaling that available from extant plants. The major drawback in reconstructing phylogenies based solely on coal-ball plants is the strong possibility that these plants represent a biased sample of Pennsylvanian environments — only those portions of lineages that had evolved the capacity to contend with the unique edaphic constraints imposed by a coal swamp would be represented. Although coal-swamp vegetation may be a sensitive indicator of climatic change, it may be a less reliable source for direct phylogenetic reconstruction of most plant groups.

Edaphic factors related to a peat substrate are probably the most important general constraint on the kinds of plants that can exploit a peat-forming swamp. Modern peat swamps are environments of low nutrient availability for living plants (Schlesinger, 1978). Much organic material is incorporated into the substrate rather than being recycled. This organic matter chelates nutrient metallic ions, thereby restricting their availability to plants once these ions enter the substrate. The pH is usually low, and water stands in the swamp for at least part of the year. These conditions require that plants be able to cycle nutrients out of the water column, as well as have physiological and morphological characteristics allowing them to grow and reproduce under aquatic to semi-aquatic, low-nutrient, low-oxygen conditions. Clastic-substrate swamps may have many of the same edaphic constraints as peat swamps. However, greater influx of water, leading to nutrient replenishment and litter decay, make flooding regime the major factor controlling plant composition (Ehrenfeld and Gulick, 1981; Conner, Gosselink, and Parrondo, 1981), resulting in differences between clastic-substrate vegetation from flooded and nonflooded sites.

The marked differences in edaphic characteristics of peat and mineral substrates result in two general classes of environments with largely different constituent populations. Vegetation and flora in moist coal-swamp environments generally differed from vegetation in surrounding clastic-substrate areas. This suggests that coal swamps were relatively distinct centers of vegetational dynamics and evolutionary change. The unique edaphic properties of the coal swamps separated them as evolutionary islands from the more intergradational vegetation of clastic lowlands and clastic swamps.

These suppositions are borne out by recent quantitative studies of coal-swamp floras (Phillips et al., 1974; Phillips, Kunz, and Mickish, 1977; Eggert and Phillips, 1982; Phillips and DiMichele, 1981; DiMichele and Phillips, n.d.; Raymond and Phillips, 1983) and of clastic compression floras (Peppers and Pfefferkorn, 1970; Pfefferkorn, Mustafa, and Hass, 1975; Scott, 1977, 1978; Pfeiffer and Dilcher, 1979; Pfefferkorn and Thomson, 1982; Winston, 1983). Coal-swamp and clastic compression floras differ markedly in the relative abundances of major plant groups and, where representatives of groups can be found in both environments, in species composition. Floras growing on clastic substrates were diverse, as Scott (1977, 1978) has shown in detail; however, there was much greater taxonomic and vegetational similarity among clastic-substrate floras than there was between clastic and peat-swamp floras. Because attainment of the ability to grow in peat swamps was a more or less evolutionarily random process, some species of nearly every major group of Pennsylvanian plants evolved the capacity to exploit effectively some kind of coal-swamp setting, with some groups being much better represented than others.

The kinds of biotic interchange that occurred between peat-swamp and clastic-substrate environments varied. For some groups there was little commonality of species from the two general classes of substrate, suggesting subsequent discretely evolving lineages. In other groups, repeated introductions of species from clastic to peat substrates occurred. Introduced species tended to remain static in some groups, whereas in other cases they were stem species of lineages that evolved further *in situ*. Populations of some species may have bridged the edaphic lines between some parts of peat swamps and nonpeat areas. For the evolutionary biologist some questions of importance thus become (1) the degree of independence between coal-swamp and non-coal-swamp evolutionary patterns and (2) the degree with which one will reflect the other. Many species of some plant groups become major elements of coal-swamp floras, whereas only a few of the many genera and species of other groups were ever significant in coal-swamp habitats. Why this may have been the case provides a fertile area for paleoecological research.

Distribution of Major Plant Groups in Coal Swamps

Five major plant groups contributed significant biomass to coal-swamp peats during the Pennsylvanian Period. The groups were arborescent lycopods, cordaites, marattialean tree ferns, pteridosperms, and sphenopsids.

Certain lycopods were dominant or subdominant throughout the Lower and Middle Pennsylvanian, disappearing abruptly in North America with the onset of the second dry interval (see fig. 8.1). The genera and species abundant in coal swamps differed from those in clastic swamps, suggesting separate centers of evolution. The arborescent lycopods constitute the only plant group in which swamp-centered lineages can be recognized clearly.

Cordaitean gymnosperms probably were adapted to periodic or long-term moisture stress, caused either by actual low substrate moisture or by "physiological drought" from brackish-water conditions. Cordaites probably were centered in clastic lowland and upland areas (Chaloner, 1958) but moved into coal swamps during times of stress due to reduced moisture.

Tree ferns and medullosan pteridosperms were minor components of coal-swamp vegetation until the late Middle Pennsylvanian. Following their appearance in coal swamps, both groups became widespread, and their abundance characterized most coal swamps after many of the lycopods became extinct at the beginning of the second dry interval. Only a few species of tree ferns and pteridosperms were able to grow in the wettest coal-swamp habitats. Species of these groups apparently were introduced into coal swamps during the first dry interval, and some lineages subsequently adapted and expanded in importance as more moisture became available. It is possible that some of the species of tree ferns and pteridosperms that were relatively rare in coal swamps may have occupied clastic-substrate areas and marginal, higher-nutrient parts of coal swamps.

The sphenopsids, such as the calamites, were not typically coal-swamp plants but were most abundant on clastic substrates, especially in clastic swamps. Calamites may not have been represented by any uniquely coal-swamp-centered species, although *Sphenophyllum* may have undergone somewhat greater differentiation (Batenburg, 1982).

In the following discussion we consider the stratigraphic distribution of these major plant groups. Relationships of the distribution patterns to changes in climate aid in the assessment of whether the variation in morphology of coal-swamp plants reflects evolutionary continua or migrations from clastic substrates into coal swamps.

Lycopods

Lycopods were the major components of coal-swamp forests during the Lower and Middle Pennsylvanian. They can be divided into two major groups with different centers of distribution and evolution. One group, centered in coal swamps, included the genera *Lepidophloios*, *Lepidodendron* of the *L. vasculare* type, and *Paralycopodites*. The other group was centered in clastic lowland areas and included *Lepidodendron* of the *L. hickii* and *L. aculeatum* type, and *Sigillaria*; species of these genera were generally rare in coal swamps but became locally abundant in parts of swamps that may have been periodically drier or higher in nutrient levels. With the onset of the second dry interval in the midcontinent region of the United States the dominant kinds of coal-swamp lycopods became extinct, but some kinds of lycopods did survive.

It is necessary to distinguish two *Lepidodendron* groups representing two distinct ecological and evolutionary entities (genera). The name

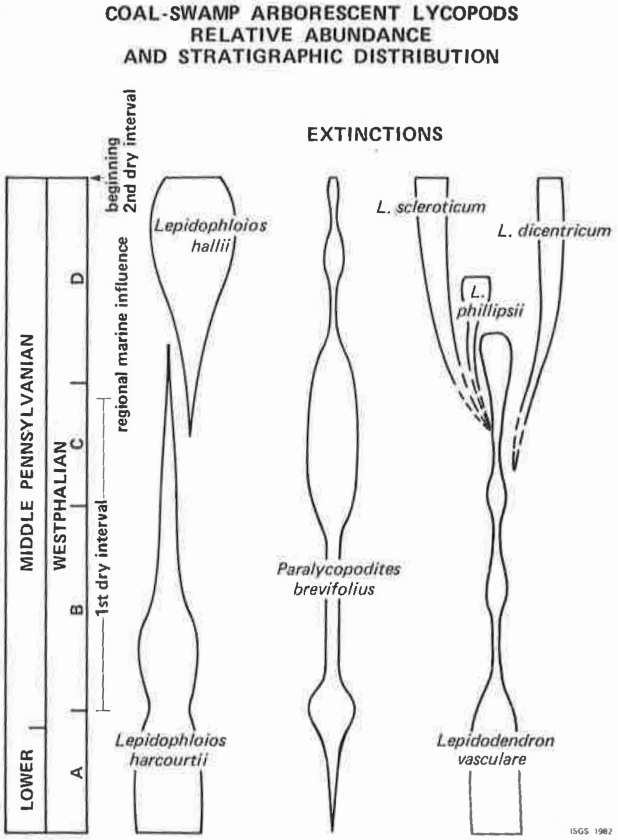

Fig. 8.2. Stratigraphic distribution and relative abundance of arborescent lycopods in Pennsylvanian coal swamps.

Lepidodendron is technically correct for the kind of arborescent lycopods centered in clastic environments, including *L. aculeatum*, which is the type species of the genus (Thomas, 1970). True *Lepidodendron* is represented in coal balls by *L. hickii* (DiMichele, 1983). Application of the name *Lepidodendron* to *L. vasculare*, *L. scleroticum*, *L. phillipsii*, and *L. dicentricum* encompasses the group of plants that paleobotanists working with coal balls have come to treat as *Lepidodendron* (DiMichele, 1981).

The lycopods, more than any other group of Pennsylvanian plants, were particularly suited to coal-swamp habitats and show great stratigraphic continuity of species in such swamps. Several evolutionary lineages of lycopods appear to have been centered in coal-swamp environments, as suggested by the markedly different relative abundances of genera and species in clastic compressions and coal-ball floras. The diversity of lycopods in coal swamps and our detailed knowledge of their morphologies allow recognition of distinct patterns of distribution and abundance changes of the major genera (fig. 8.2), patterns that correlate generally with climatic fluctuations.

Lepidophloios. *Lepidophloios* was the most highly aquatically adapted of the arborescent lycopods. The reproductive structures of *Lepidophloios* (*Lepidocarpon*) and the general vegetative morphology of the plant (Phillips, 1979; DiMichele and Phillips, n.d.; DiMichele, 1979a) reflect this aquatic adaptation. Community paleoecology indicates that *Lepidophloios* was strongly dominant (more than 70 percent of biomass) in low-diversity communities having relatively few free-sporing and ground-cover plants (Phillips and DiMichele, 1981). As a consequence of extreme aquatic adaptations, and the abundance of *Lepidophloios* in coal swamps, its distribution reflects more closely the prevailing climatic wetness than does the distribution of the other arborescent lycopods.

Lepidophloios harcourtii was relatively widespread and abundant in Lower Pennsylvanian (Westphalian A) coal swamps of England and elsewhere in western Europe during a time of moderately wet, monsoonal climate (Broadhurst, Simpson, and Hardy, 1980). There was a general decline in its abundance at the onset of the first major dry interval of the Pennsylvanian, a time from which it has been identified in coals of eastern Kentucky, eastern Tennessee, and Iowa. The total contribution of *L. harcourtii* to peat biomass during this period varies greatly, based on the study of the few coals we have sampled. It appears that the once rather extensive stands of *L. harcourtii* in the Lower Pennsylvanian swamps may have been replaced by smaller populations that were spatially and temporally isolated. During the late Middle Pennsylvanian *Lepidophloios*-dominated swamps increased in frequency and areal extent to become the most common kinds of coal swamps. Coinciding with this reexpansion of *Lepidophloios* swamps, *L. harcourtii* was replaced by *L. hallii* as the predominant form in coal basins of midcontinental United States (figs. 8.2 and 8.3). *Lepidophloios* began to decline just prior to the beginning of the second dry interval, at which time it became extinct.

A shift in the predominant species of *Lycospora* occurred during the first dry interval of the Pennsylvanian (Peppers, 1979; Phillips and Peppers, n.d.). *Lycospora* is the microspore of *Lepidophloios* and several other lycopod genera. A shift in dominance from *Lycospora pellucida* to *L. granulata* coincides with the *Lepidophloios harcourtii–L. hallii* shift. However, the considerable overlap of the two microspore species in space and time suggests that this was not an abrupt ecological replacement. It is possible that *L. hallii* evolved in coal swamps from an

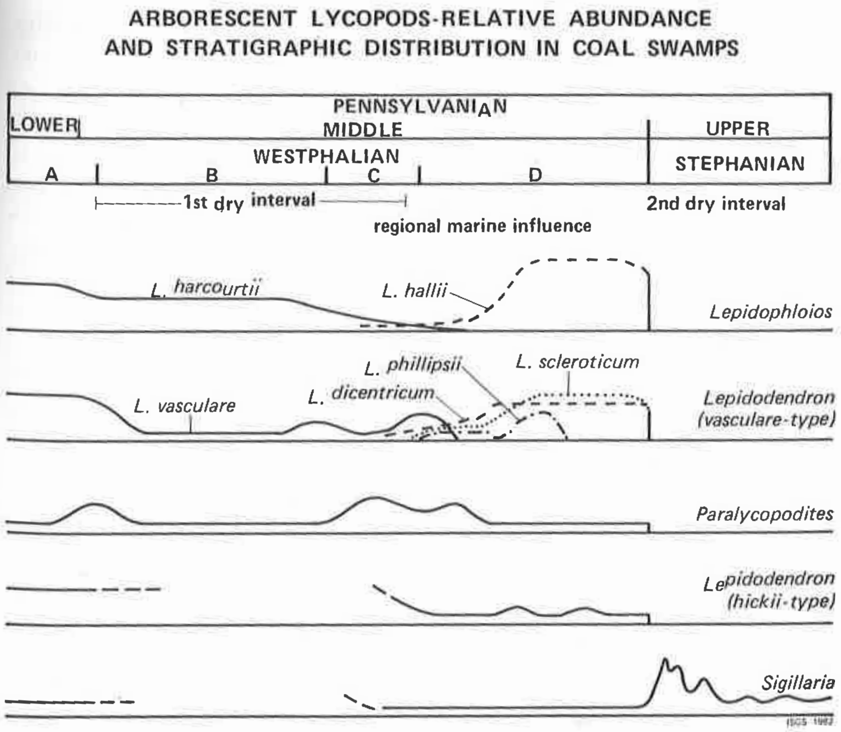

Fig. 8.3. Stratigraphic distribution and relative abundance of arborescent lycopods in Pennsylvanian coal swamps.

isolated population of *L. harcourtii*, incorporating the slight but consistent morphological differences between these two species (DiMichele, 1979a).

Lepidodendron (*L. vasculare* type). Four species of *Lepidodendron*, comprising two morphological groups, have been identified in coal balls. *Lepidodendron vasculare, L. scleroticum*, and *L. phillipsii* are morphologically similar and are distinct in several character states from *L. dicentricum*. The kind of morphological organization represented by these species is more common in coal balls from coal-swamp deposits than it is in compression floras from clastic-substrate areas. This may indicate that evolution in this genus was centered largely in coal swamps rather than in clastic swamps, although we cannot rule out introductions from clastic swamps as a source of changes in the composition of coal-swamp species through time. All four species produced *Achlamydocarpon varius* cones and *Capposporites distortus* microspores.

Although *Lepidodendron vasculare, L. scleroticum*, and *L. phillipsii* were morphologically similar, each species showed little intraspecific morphological variability. All produced small numbers of cones on deciduous lateral branches borne on an excurrent trunk (DiMichele, 1981). This provided them with the capacity to occupy sites subject to irregularly occurring, severe perturbations because reproduction was essentially continuous, providing a constant local background of propagules. Palynological studies (Peppers, 1979) indicate that *Capposporites* increased in abundance in areally discontinuous coal swamps or swamps that seem to have had peat deposition interrupted by transgressions or floods, regardless of the regional climatic trends.

During the Lower Pennsylvanian (Westphalian A) and up to the onset of the first dry interval, *Lepidodendron vasculare* was the only major species of the genus in coal swamps (fig. 8.2). According to megafossil samples, *Lepidodendron* was very rare in swamps during the drier period, although palynological studies indicate that it was locally abundant. During the period of increasing wetness, *L. vasculare* again became a major component of coal swamps. In the eastern regions of the Illinois Basin Coal Field, *L. vasculare* dominated small brackish swamps. It was a minor component in the Western Interior Coal Region (Iowa and Oklahoma). Occurring in conjunction with *L. vasculare* in some of these swamps were rare specimens of *L. phillipsii* and *L. scleroticum*, the earliest known appearances of these plants in coal balls. These species subsequently replaced *L. vasculare* as the areal extent of swamps and freshwater availability increased during the middle Westphalian D. *Lepidodendron phillipsii* reached maximum abundance locally in the Colchester (No. 2) and Summum (No. 4) Coal Members of Illinois, which palynology suggests were mostly dominated by *Lepidophloios* (Peppers, 1970). In these areas *Lepidodendron phillipsii* may have been growing in more elevated, perhaps drier regions of peat deposition. *Lepidodendron scleroticum* expanded as a component of *Lepidophloios hallii*–rich coal swamps. It is likely that *L. scleroticum* and *L. phillipsii* evolved from populations of *L. vasculare* during the first dry interval. These two species are similar to *L. vasculare* and may have displaced it as the areal extent of swamps increased in the late Middle Pennsylvanian (fig. 8.3). This pattern is similar to that suggested for *Lepidophloios*, but with more species involved.

Lepidodendron dicentricum trees had dendritic, determinate crowns with a large number of synchronously produced terminal cones (DiMichele, 1979b, 1981). The trees probably were spaced rather widely in coal swamps and were minor contributors to the biomass except where they occurred in assemblages of high diversity. This pattern is indicative of a fugitive ecological strategy. The species exhibits relatively high intraspecific morphological variability, which is a function of the presence of brackish and nonbrackish ecotypes (DiMichele, 1978, 1981).

The pattern of distribution of *Lepidodendron dicentricum* bears little relationship to those of the other species of *Lepidodendron*. Its earliest known stratigraphic occurrence is in eastern Tennessee in the middle Middle Pennsylvanian during a time of increasing wetness. *Lepidodendron dicentricum* occurs in small numbers until the time of major expansion of *Lepidophloios hallii*–rich swamps, in which it became a consistent but minor component. Stratigraphically, the brackish-water ecotype of *L. dicentricum* predominated early in the midcontinent swamps that were of relatively limited areal extent and proximate to marine conditions. As increase in the wetness and areal extent of swamps occurred, the brackish-water ecotype became restricted in distribution to the later phases of peat deposition in some swamps, while the freshwater form became more common. The later stages of these freshwater coal swamps may have been drier or under the influence of slightly brackish conditions prior to marine transgression.

Paralycopodites. *Paralycopodites* was an uncommon component of most coal-swamp vegetation. It became a major element in some swamps during the first dry interval and occurred sporadically after that time, prior to its extinction at the end of the Middle Pennsylvanian (fig. 8.2).

All specimens of *Paralycopodites* are morphologically very similar, and only a single species, *P. brevifolius* (DiMichele, 1980), is recognized. This small tree is associated with two species of cones in the Middle Pennsylvanian, *Flemingites schopfii* (Black, 1970) and *F. diversus* (Felix, 1954). *Flemingites schopfii* occurs in eastern Kentucky and differs in minor but consistent ways from *F. diversus*, which is found in the Eastern Interior Coal Province. This may indicate the existence of two (or more) species in coal swamps that otherwise did not differ detectably in vegetative morphology. Peat and palynological studies suggest that *Paralycopodites* was the major source of *Lycospora micropapillata*. Increases in the abundance of this spore correspond closely to increases in abundance of *Paralycopodites* in coal balls during the first dry interval. *Paralycopodites* grew largely in coal swamps, probably in areas of irregularly fluctuating low-water levels; the compression equivalent to *Paralycopodites* was probably *Ulodendron* (*sensu*, Thomas, 1967), a rarely encountered form.

Sigillaria and *Lepidodendron* (*L. hickii-aculeatum*). *Sigillaria* and true *Lepidodendron* were not centered in coal swamps. They are represented by numerous compression species that were common in a variety of clastic wetlands. The presence of species of these genera in coal swamps during the Lower and Middle Pennsylvanian suggests unusual conditions, perhaps involving increased clastic influx or seasonal dryness. Both genera are locally abundant in Lower Pennsylvanian (Westphalian A) coal balls of Europe. There are some indications from coal-ball and palynological data that these genera occurred locally in coal swamps during the first dry interval (fig. 8.3).

Lepidodendron hickii is a more significant coal-swamp element than *Sigillaria* in the Lower Pennsylvanian and in most Middle Pennsylvanian swamps where both occur. Occurrences in coal balls commonly are associated with local fluvial activity, as indicated by splitting of the coal by freshwater shales and sandstones. This suggests growth of *L. hickii* in rare nutrient-rich areas, possibly with great freshwater influx. The extinction of *L. hickii* and other species of true *Lepidodendron* at the end of the Middle Pennsylvanian in the midcontinent may be due to elimination of the clastic swamps in which they were most abundant. Such environments would have been affected by a regional decline in available moisture in much the same way as coal swamps. The almost complete, if temporary, elimination of the adaptive zone of coal- and clastic-swamp trees would have left few populations to recolonize swamps when favorable conditions returned and may be the key to extinction of such forms.

Species of *Sigillaria* occurred sporadically in Lower and Middle Pennsylvanian coal swamps, usually in association with indicators of drier coal-swamp conditions (Phillips and DiMichele, 1981). The survival of *Sigillaria* into the Upper Pennsylvanian of the midcontinent, despite the onset of the second, more severe, dry interval, may be due to the adaptation of many species to growth in mesic lowland areas that were not necessarily swamp habitats. Thus, a diversity of ecological tolerances among the species circumscribed a broad adaptive zone for the genus allowing persistence. *Sigillaria* is so uncommon in Middle Pennsylvanian coal-ball floras that species have not been delimited on the basis of anatomical data. It is not known whether Upper Pennsylvanian species of *Sigillaria* in coal swamps were carry-overs from Middle Pennsylvanian coal swamps or were later introductions from surrounding lowlands. Considering the lycopod extinctions at the second dry interval and the abundance of *Sigillaria* in compression floras, it seems probable that Upper Pennsylvanian species represent a reintroduction of the genus into coal swamps.

Cordaites

Cordaitean gymnosperms were important elements of coal-swamp vegetation during the first dry interval of the Pennsylvanian and during the period of regional brackish influence in midcontinent coal swamps that accompanied the subsequent increasing wetness (fig. 8.4). The group was able to enter coal swamps from surrounding lowlands during these times perhaps because of a general ability to grow under conditions of moisture stress (Wartmann, 1969). Two cordaitean genera were important in coal-swamp habitats — *Mesoxylon*, parent of *Mitrospermum* ovules, and *Pennsylvanioxylon*, which produced the ovule *Cardiocarpus*. Species of these genera probably had different tolerances to the parameters of moisture stress and brackishness. Basing their analysis on Iowa coal-ball floras, Raymond and Phillips (1983) suggested that the species of *Pennsylvanioxylon* that produced *Cardiocarpus spinatus* (and possibly one that produced *C. magnicellularis*) had the greatest tolerance of brackish conditions; *Mesoxylon*, although tolerant of decreased moisture availability, was not abundant in assemblages that were subject to marine influence or long-term brackish conditions. These conclusions, are supported by the stratigraphic distribution, the timing of appearances relative to climatic fluctuations, and the kinds of assemblages in which the species occurred. Another species of *Pennsylvanioxylon*, which produced *Cardiocarpus oviformis*, occurs in assemblages that appear to have been subjected to little or no brackishness,

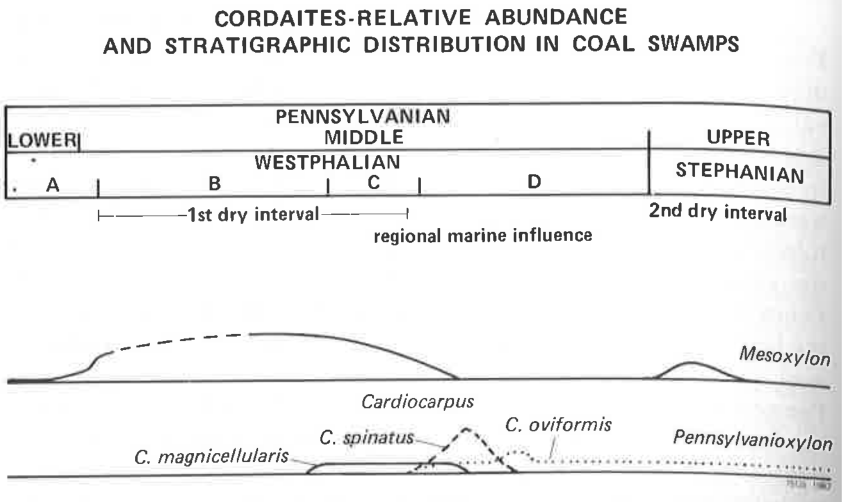

Fig. 8.4. Stratigraphic distribution and relative abundance of cordaites in Pennsylvanian coal swamps.

particularly from coals of the upper Middle and Upper Pennsylvanian.

Mesoxylon was relatively rare in coal swamps prior to the first dry interval. Coal balls in which *Mesoxylon* is abundant have high root-shoot ratios and show evidence of extensive decay of aerial litter. This suggests growth in those parts of coal swamps that may have been the most periodically dry. *Mesoxylon* was replaced as the major cordaite in coal swamps largely by *Pennsylvanioxylon* during the period of increasing wetness and concurrent brackish influence in the middle Middle Pennsylvanian. *Mesoxylon* occurred again in some coal swamps of the Upper Pennsylvanian during the second dry interval (fig. 8.4).

Pennsylvanioxylon first appeared in coal swamps during the first dry interval (Westphalian B). The earliest ovules recorded are *Cardiocarpus leclercqii* (= *C. magnicellularis*) from coal k_8 of the Donets Basin (Snigirevskaya, 1972) and the Aegir Horizon (Westphalian B-C boundary) of the Netherlands (Koopmans, 1934). However, it was not until later in the Middle Pennsylvanian that a *Pennsylvanioxylon* species, producing *C. spinatus*, reached its peak abundance in coal swamps that were subject to some brackish influence. These plants have been interpreted as small mangrovelike trees (Cridland, 1964; Costanza, 1981). This abundance was short-lived, and the *C. spinatus* producers declined rapidly with the advent of extensive freshwater swamps. The *Pennsylvanioxylon* that produced *Cardiocarpus oviformis* continued to be present in coal swamps through the upper Middle and

Upper Pennsylvanian. It was relatively abundant in parts of the Colchester (No. 2) and Summum (No. 4) Coals of Illinois, where *Lepidodendron phillipsii* was dominant, areas that presumably had the greatest elevation and fluctuations in water level in the swamps. Rothwell and Warner (n.d.) have reconstructed the *C. oviformis* producer is a small, shrubby plant in the Upper Pennsylvanian–age Duquesne Coal of Ohio.

The distribution of cordaites and the major areas of cordaite evolution are unresolved. The morphology of the plants suggests that they were xerophytes (Wartmann, 1969), and paleoecological studies support this conclusion (Peppers and Pfefferkorn, 1970; Scott, 1977; Raymond and Phillips, 1983). However, it is not clear if diversity and major evolution in the group was centered in "upland" (nonbasinal) areas (Chaloner, 1958) or whether the group was actually very diverse and widespread, with both lowland and upland components, possibly representing independent evolutionary lineages. If cordaites were centered primarily in uplands and mesic lowlands, the record of these plants in coal balls contains some serious phylogenetic gaps. These gaps may be least serious for *Pennsylvanioxylon*, which was possibly a coal-swamp-centered form. The three species of *Cardiocarpus* found in coal swamps overlap stratigraphically and vary from each other in minor ways, and the morphology of the species even varies regionally, suggesting that morphological variation originated in the swamps.

Medullosan Pteridosperms

The dominance of medullosan pteridosperms in many compression floras throughout the Pennsylvanian indicates that they were centered in mesic lowlands; only rarely were medullosans dominant in coal-swamp floras. *Medullosa* was a minor component of early Westphalian A coal swamps of Europe. This small but consistent representation continued throughout the early Middle Pennsylvanian in coal swamps in Illinois and the Appalachian Basin during the first dry interval. With increasing wetness in the late Middle Pennsylvanian, *Medullosa* became more abundant in coal swamps, an increase that correlated closely with the expansion of *Lepidophloios hallii*–rich swamps. At the time of their most extensive occurrences in the Middle Pennsylvanian, medullosans accounted for 10–15 percent of coal-swamp peat biomass. However, they were locally even more abundant, and their distribution was probably very discontinuous in coal swamps (Phillips, Kunz, and Mickish, 1977; Phillips and DiMichele, 1981). Medullosans became second in importance to tree ferns during the Upper Pennsylvanian.

Foliage is the most abundant kind of medullosan organ preserved and indicates, in a general manner, the amount of taxonomic overlap between coal-swamp and compression forms. All the species of *Neuropteris* or *Alethopteris* that have been identified in coal balls also occur in compression floras. These include *Neuropteris rarinervis* (Oestry-Stidd, 1979), *Neuropteris scheuchzeri* (Reihman and Schabilion, 1979), *Alethopteris lesquereuxii* (Baxter and Willhite, 1969), *Alethopteris sullivantii* (Leisman, 1960), and an *Alethopteris* much like *A. serli* (Mickle and Rothwell, 1982). *Mariopteris* (Stidd and Phillips, 1973), *Sphenopteris obtusiloba* (Shadle and Stidd, 1975) from the lyginopterid *Heterangium*, and *Linopteris* (Stidd, Oestry, and Phillips, 1975) also have been identified in both coal balls and compressions. In addition, there is a general overlap in size and shape of petrifaction and compression ovules. These features suggest that some of the same kinds of medullosans inhabited coal swamps as clastic-rich environments.

Medullosans probably grew in parts of coal swamps that were drier and higher in available nutrients than the lycopod-dominated parts of coal swamps. Quantitative studies of coal balls (Phillips, Kunz, and Mickish, 1977; Phillips and DiMichele, 1981) indicate that assemblages with more than 20 percent *Medullosa* are among the highest in fusain of any coal-swamp assemblages, indicating fires or peat oxidation and suggesting exposed substrates. Coal adjacent to coal-ball peat dominated by *Medullosa* is commonly high in mineral matter (Johnson, 1979), suggesting influx of clastics in floods or perhaps peat decay, which concentrates mineral matter.

The first dry interval fragmented and disrupted coal-swamp community structure, which may have rendered coal swamps more seasonally dry and edaphically heterogeneous. Under such conditions populations of medullosans could have established in coal-swamp communities more easily. With subsequent increased wetness and development of large, environmentally heterogeneous coal swamps, medullosan populations in coal swamps increased. Evidence from paleochannel environments suggests that levees supported larger stands of medullosans than generally were present in parts of coal swamps distant from channels. The overlap of coal-ball and compression foliage suggests that little intraswamp speciation occurred and that in some species there was overlap between clastic and coal-swamp populations.

Interpretation of the coal-ball record of the medullosans as a reliable, direct indication of phylogenetic patterns has great potential bias. If the establishment of medullosans in Middle Pennsylvanian coal swamps is primarily a product of random unidirectional introductions from mesic lowlands during periods of climatic disruption of swamp communities, then the coal-ball record is likely to represent a small, ecologically biased sample of the group. In this case, it would be difficult to track evolving lineages because of great incompleteness of the coal-ball record. On the other hand, if free exchanges occurred between clastic substrates and marginal, nutrient-rich or drier parts of coal swamps, then for some groups coal-ball floras may reflect general patterns of change. At present it appears that medullosan diversity in mesic lowland environments was much greater than that in coal swamps. Although some species were represented in both general classes of environments , coal swamps did not reflect total medullosan diversity. Thus, general evolutionary trends in the group may be deduced from coal balls, but it would appear that significant, ecologically mediated biases exist.

Marattialean Ferns

Marattialean ferns, like medullosan pteridosperms, are a morphologically and taxonomically complex and diverse group that occurs extensively in compressions and coal balls. Their pattern of distribution in coal swamps parallels that of the medullosans and suggests similar ecological mediation of distribution.

Psaronius tree ferns occurred sporadically and in limited numbers in coal swamps during the Lower Pennsylvanian. According to palynological data, they diversified in regions outside coal swamps during the first dry interval in the early Middle Pennsylvanian, a diversification accompanied by introduction of a few additional forms to coal swamps (Peppers, 1979). *Psaronius* became a significant component of coal-swamp vegetation, as 5–10 percent of the peat biomass, during middle Middle Pennsylvanian time in the Illinois Basin. In the late Middle Pennsylvanian swamps *Psaronius* attained maximum abundance in widespread, freshwater *Lepidophloios*-rich coal swamps and in cordaite-dominated coal swamps subject to brackish influence. In Upper Pennsylvanian swamps *Psaronius* was usually the dominant element. At present it appears that few of the species important in Middle Pennsylvanian coal swamps persisted into the Upper Pennsylvanian.

The best indications of marattialean taxonomic diversity are reproductive structures, which are difficult to correlate between compressions and petrifactions. Millay (1979, 1982) has approached this problem by comparing fertile pinnule morphology, the general aspect of sporangial placement, and palynology. He has found that many of the general groups of pecopterid foliage delimited by Corsin (1951) for compressions can be recognized in petrifactions, but that most coal-ball forms are similar to the *Pecopteris arborescens* group. Representation of the other groups is sparse and often rare. This scarcity suggests that a relatively small number of marattialean species accounts for most of the *Psaronius* biomass found in coal swamps. Quantitative studies of the Summum (No. 4) and Herrin (No. 6) Coals in the Illinois Basin indicate that, in these coals, most of the marattialeans are accounted for by the *Scolecopteris minor* group or *S. parvifolia* of Millay (1979); other species account for little of the total *Scolecopteris* biomass. Taxonomic studies indicate that marattialean diversity was generally low in any single coal swamp and that some species were restricted regionally.

Marattialeans are known to have had a long evolutionary history prior to their becoming major constituents in coal swamps. The earliest forms from the Upper Mississippian and Lower Pennsylvanian had simple monocyclic stelar architecture (DiMichele and Phillips, 1977). Increased anatomical complexity is first indicated by the presence of polycyclic stems that occur in nodules in shales above coals in the Westphalian A of England, suggesting that evolution of this anatomy occurred in mesic lowland habitats rather than in coal swamps. *Psaronius* was not a major part of coal-ball floras until the middle Middle Pennsylvanian; however, palynology provides insight into the diversification of marattialeans, which may have occurred during and immediately after the first dry interval (Peppers, 1979; Phillips and Peppers, 1984). The palynological data were derived from coals; however, coals of the first dry interval were areally restricted. Small coal swamps likely received abundant pollen and spore rain from adjacent areas and provide evidence of regional patterns of diversity. Thus, these coals may well reflect evolutionary diversification of this group in surrounding clastic wetlands rather than in coal swamps. If this were so, the later appearance of abundant *Psaronius* in coal-ball floras may reflect its subsequent invasion of coal swamps and expansion to levels detectable by coal-ball sampling.

Marattialean diversification and subsequent introduction into coal-swamp floras is difficult to interpret due to apparent conflicts in the lines of evidence. Data from coal palynology suggests a diversification in the early Middle Pennsylvanian; the tree ferns are presumed to be in, or marginal to, coal swamps. However, this is not corroborated by coal-ball studies or by analysis of compression-impression floras. According to megafossils marattialeans first became common in wetland areas during the late Middle Pennsylvanian (Pfefferkorn and Thomson, 1982; Phillips and Peppers, 1984). This suggests that the diversity of tree-fern spores in the early Middle Pennsylvanian coals was derived from regions in which preservation of megafossils was unlikely, possibly in lowland areas but in places with fully exposed soils. Taxonomic studies of fructifications show that many marattialean species occurred in coal swamps in general, but they also suggest that there was regional variability, with only a few species making a significant contribution to biomass. A few evolutionary lineages may have become centered in coal swamps after the radiations of the first dry interval. Species of these lineages had broad ecological amplitudes and were evolutionarily conservative. They persisted at least until the end of the Middle Pennsylvanian. Also occurring in the same swamps were less common species that were parts of lineages centered in clastic-wetland areas but that had the potential to occupy marginal parts of coal swamps.

Sphenopsids

Sphenopsids were represented in coal swamps by two major evolutionary groups, the arborescent calamites and the shrubby or viney *Sphenophyllum*. Both groups of sphenopsids occurred in coal swamps and were locally abundant or even dominant in clastic-substrate areas. Calamites are usually characterized as hydrophytes that grew along the margins of lakes or streams in shifting substrates and that were tolerant of periods of standing water (Scott, 1977, 1978). *Sphenophyllum* may have been more variable, growing in less frequently submerged areas (Batenburg, 1981). These deductions are supported by evidence from shale deposits in which calamite stems are often thickly layered or in which *Sphenophyllum* is preserved three-dimensionally through a considerable thickness of rock.

The presumed growth habit of both calamites and *Sphenophyllum*, spreading by the growth of rhizome systems, may explain their localized abundance in many compression floras. The calamites are the only group of Pennsylvanian arborescent lowland plants that had this potential for extensive vegetative propagation, which, like their modern counterpart, *Equisetum*, would have permitted them to colonize areas with unstable substrates. Their production of spore-bearing cones may have provided an effective means of dispersal to such colonizing plants occupying marginal, open-water areas.

Sphenophyllum was widespread and commonly occurred in swamps through most of the Pennsylvanian. Batenburg (1982) has suggested that there was an ecological differentiation between coal-swamp and clastic-lowland species, with little taxonomic overlap between the two general environments. Due to the small size of the plants, the species that grew in coal swamps were not significant contributors to the peat biomass. The calamites were also common throughout the Pennsylvanian in coal swamps, and despite their occasional large size (we have found stems at least 45 cm in diameter), their biomass contribution was low and confined to a few kinds of swamp assemblages often rich in *Medullosa* or *Sigillaria*. Palynology (Peppers, 1979) indicates an increase in abundance of calamites in some coal swamps, particularly during parts of the first dry interval, but this is exceptional. Fusinized preservation of calamite organs is common, and peat layers containing abundant calamite roots are frequently more common than those with abundant stems. Perhaps calamites were common in areas where decay of aerially exposed peat was pronounced, leaving few aerial remains that were commonly fusinized.

Calamites were probably centered outside coal swamps. They grew on loosely consolidated, shifting substrates, such as sand bars or stream and lake margins — habitats especially suited to rhizomatous plants. Where comparisons can be made, particularly on the basis of reproductive structures, it appears that there was a general overlap between coal-swamp and clastic-lowland forms. Only the genus that bore *Calamocarpon* (functionally monosporic megasporangia) was apparently persistent in coal swamps, but it was not very abundant.

Discussion

Pennsylvanian coal swamps were largely self-perpetuating, edaphically constrained habitats in the midst of the tropical lowlands; they were characterized by low taxonomic diversity and by the dominance of lower vascular plants. Although probably not important sites of evolutionary change (speciation), these swamps may have been evolutionary refugia for many lower vascular plant groups dependent on moist environments. Changes in vegetation during the Pennsylvanian were controlled in part by changing climatic patterns, particularly fluctuation in freshwater availability (net rainfall, runoff, and evapo-transpiration). Because of the "edaphic-island" nature of coal swamps, the changes in vegetation are excellent indicators of general trends in climatic conditions. However, edaphic factors excluded and many plants from coal swamps; thus, evidence from coal-swamp plants is an uncertain indication of the actual evolutionary patterns and morphological changes that accompanied individual speciation events within many phylogenies. Of the five major plant groups in coal swamps, the lycopods and ferns had the most endemic species, and it seems likely that only in the lycopods were some evolving lineages strongly centered in coal swamps.

The four major kinds of changes affecting the composition of coal-swamp vegetation during the Pennsylvanian (expansions, migrations and introductions, extinctions, and evolution) were most pronounced during times of marked climatic change. Quantitative shifts in the abundances of endemic coal-swamp trees are the major bases for paleoecological inferences about coal swamps. Frequently, the changes in the abundances of coal-swamp-centered species were coupled with the increasing abundance of newly introduced forms or new species. Migrations and introductions of plants into coal-swamp habitats from surrounding mesic or swampy lowlands probably account for most of the increased diversity in coal swamps during the Pennsylvanian. Introductions, which occurred during relatively short and defined periods, involved mainly the tree ferns, pteridosperms, and cordaites. These introductions coincided with times of inferred stress due to reduced moisture. The most obvious changes in composition of coal-swamp floras resulted from extinctions of major plant genera, which occurred during the Lower-Middle and Middle-Upper Pennsylvanian transitions. These extinctions included several arborescent lycopods and possibly many fern and pteridosperm species.

It is difficult to document evolution within coal-swamp ecosystems. It is often conjectural as to where, when, and under what ecological conditions new species appeared and to what degree their detection is affected by taphonomy. From an examination of changes in plant morphology in a given lineage through the entire Pennsylvanian, it is clear that evolutionary change took place. However, what makes phylogenetic inferences based on coal-swamp plants so precarious is the "island" nature of coal swamps, which preserve only parts of evolutionary lineages. Thus, morphological change observable within coal-swamp plants *per se* cannot be equated with direct lineal descent. Ancestor-descendant lineages are perhaps best represented in the lycopods. For most other plant groups the coal-swamp record may be one of isolated and random introductions of distantly related parts of evolving lineages that were centered outside coal-swamp habitats. Such a pattern of ecological distribution compounds the problem faced by paleontologists in reconstructing evolutionary (ancestor-descendant) relationships of organisms (Patterson, 1981), something that is inherently not falsifiable and that has received considerable discussion in the recent literature of systematic zoology.

Climate and Changes in Vegetation

The relative importance of the four major factors influencing the floristic composition of coal swamps differed during the two periods of vegetational change. As a result, these two periods of change represent two different kinds of events. During the first drier interval, introductions and subsequent quantitative shifts in abundance were most important and perhaps were linked to evolution of new taxa. Extinctions were of limited importance. The second dry interval was more severe; extinctions were pronounced and led to drastic quantitative shifts in composition of swamp floras. Subsequent introductions appear to have occurred in what were distinctly different kinds of coal swamps from those of the Middle Pennsylvanian. As indicated by the appearance of new species, the amount of evolution at this time was much greater in mesic lowland habitats than in coal swamps. However, our inability to discern evolutionary change within Upper Pennsylvanian coal swamps may also result in part from a lack of understanding of plants of this age. Palynology of coals in the Upper Pennsylvanian of the Illinois Basin has not been studied in as much detail as in the Middle Pennsylvanian.

First Dry Interval — Early Middle Pennsylvanian

The dry interval of the early Middle Pennsylvanian and the subsequent period of increasing moisture availability seem to be the major times during which evolutionary change occurred within Pennsylvanian coal swamps. It was in this period that maximum quantitative shifts in dominant and subdominant species occurred (but without loss of important genera, except for *Lyginopteris*) and that several groups appear to have been introduced into coal-swamp environments from the surrounding wetlands and mesic lowlands. The newly introduced groups rose to importance rapidly or expanded at a slightly later time as wetness and habitat heterogeneity in swamps increased. Cordaites were the first group to increase in abundance during the dry interval, followed by increases in tree ferns and then medullosan pteridosperms. All these groups were present to some extent in Lower Pennsylvanian coal swamps, and their increases may have involved expansion of endemic coal-swamp forms as well as introduction of species from surrounding lowlands.

The nature of the events leading to the floristic and vegetational changes of the Middle Pennsylvanian coal swamps is suggested as follows. (1) Decreased moisture availability, accentuated by seasonal dryness, resulted in contraction in area and time of duration of coal swamps. (2) Coal swamps were increasingly isolated from each other in the lowlands and were less edaphically distinctive from other wetlands; such coal swamps were "drier" with increased peat oxidation and decay.

(3) Swamp communities were progressively disrupted due to shrinking of physical settings conducive for coal-swamp development. Such swamps probably increased in heterogeneity, both spatially and temporally, accentuating the nonequilibrial aspects of community structure and resulting in incomplete utilization of available resources (Pickett, 1980).

These events would produce several different consequences. (1) The floristic composition of separate coal swamps during the dry interval should have been variable. (2) Plants from the surrounding lowlands, particularly clastic wetlands, may have been able to exploit coal-swamp resources because of the increased heterogeneity of coal-swamp habitats. (These previously had been excluded from the coal swamps because of the waterlogged soils and general environmental homogeneity, features that favored the establishment of low-diversity, "equilibrium" vegetation.) The coal swamps may have become mosaics of saturated and unsaturated substrates due to periodic drying of the peat, allowing some plants from clastic lowlands undergoing stress due to decreasing moisture to move into coal swamps. (3) For similar reasons, new species evolving in the lowlands, as well as in the swamps, would have had a greater chance of locating suitable habitats during these times of disruption of coal-swamp communities.

The genetic origin of variation is a continuously occurring process, providing the phenotypes that are the raw material of the morphological divergences we detect as speciation. However, one of the major constraints on the amount of speciation we detect is the ability of newly evolved lineages to survive and become established in the ecosystem. Barriers to establishment of new species in coal swamps should have been lowest during the first dry interval. If the species changes in coal swamps that we detect during this time period are due largely to establishment of newly evolved forms, we would find a pattern similar to that described by Williamson (1981) for mollusks in the Turkana Basin of East Africa — that is, proliferation of new morphotypes during times of increasing isolation and fragmentation of ancestral populations in combination with increasing environmental stress. The fossil record of the plants of this part of the Pennsylvanian is much less complete than that of Williamson's mollusks, and the ancestral species do not return to displace their descendants as climate moderates. However, the general similarities of mass morphological change correlated with a specific set of ecological changes is an interesting and noteworthy parallel.

At the end of the first dry interval, there would have been many locally established populations that had been introduced to coal swamps or that had expanded in abundance within coal swamps. These would have competed for increasing swamp resources. There also would have been fragmented populations of formerly dominant plants, such as the lycopods *Lepidophloios hallii* and *Lepidodendron vasculare*. These also may have given rise to new species populations due to long-term isolation and consequent genetic drift. Along with these plant populations were groups, such as the cordaites, that had risen to abundance during the drier interval because of their ability to cope with moisture stress.

As coal swamps became wetter and less seasonally limited and as available resources expanded, the competitive sorting-out of these species resulted in coal swamps with a different vegetation and flora than those that preceded the onset of dryness. The major swamp lycopods remained part of coal-swamp communities during the dry interval; with increasing wetness the earlier species were replaced by new but morphologically similar forms. Palynology indicates that fern diversity rose sharply during the driest part of the interval, when mesic lowlands were also under moisture stress. However, tree ferns do not appear in coal balls until the later Middle Pennsylvanian, as moisture availability increased. We lack the benefits of a precise palynological record of medullosan pteridosperms during the dry interval. Nevertheless, their later appearance in coal-swamp communities paralleled that of the ferns and suggests somewhat similar ecological constraints. The cordaitean genus *Mesoxylon* increased in abundance during the dry interval, a pattern consistent with the concept of cordaites as "upland"-centered plants adapted to drier sites. It declined in abundance with increasing wetness in the late Westphalian C.

The pattern of change in the transition from the first dry interval to more continuously wet conditions is complicated regionally by periods of influence of brackish water in midcontinental coal swamps. This brackish influence caused a short-term decline in diversity and a rise in brackish-tolerant plants, such as some species of *Pennsylvanioxylon* (*Cardiocarpus spinatus*). This further complicates the picture of evolution and introduction at this time. It is during the later phases of this brackish interval that tree ferns and medullosans became significant elements in lycopod-dominated swamps.

Second Dry Interval — Middle-Upper Pennsylvanian Transition

The consequences of the second dry interval are considerably different from those of the first because of the greater severity of climatic change. With the onset of second dry interval, the areal extent of coal swamps and their temporal duration diminished dramatically in comparison with those of the Middle Pennsylanian. There may even have been a brief period when coal swamps were almost nonexistent. We interpret the effects of the second, severely dry interval as follows. (1) Coal swamps were greatly reduced in areal extent and duration at least for some time prior to return of favorable conditions. (2) Swamps had much reduced areas of long-standing water. Seasonal moisture and runoff would have been sufficient to allow peat accumulation to occur, but parts of these swamps would probably have suffered long, seasonal dry-downs. (3) Vast areas would have been inundated by the sea during transgression, thus eliminating much of the potential swamplands.

The biological effects of the second dry interval are clear. All the major arborescent lycopods of the coal swamps and most of them from the clastic-swamp areas became extinct in the midcontinental coal basins. From this extinction we deduce that the wettest freshwater portions of coal swamps, which were dominated by arborescent lycopods, were eliminated. It is also probable that there were major extinctions of tree fern and medullosan species and that the effect of the climatic drying was the nearly complete elimination of coal swamps. The lack of detailed taxonomies for these latter groups makes interpretation of their patterns of change more difficult than for the lycopods. There was also a significant reduction in coal-swamp plant diversity and in the structural diversity of the vegetation. Tree ferns rose in importance and became dominant in most swamp communities, achieving the levels of dominance equal to or greater than those seen for lycopods in the late Middle Pennsylvanian. Medullosans were second in importance. The floristic similarity of the clastic lowland environments and coal swamps was high, and it is more difficult to differentiate coal-swamp from clastic-substrate vegetation after the second dry interval than at any other time during the Pennsylvanian. Marshes, dominated by *Chaloneria* with abundant *Sphenophyllum*, became ephemeral contributors to peat-forming wetlands.

The evolutionary consequences of the second dry interval are not clear. Our present taxonomic concepts for tree ferns and medullosans do not provide an adequate basis for determining their quantitative differences in late Middle Pennsylvanian and Upper Pennsylvanian coal swamps or differences between clastic and coal-swamp environments. However, the presence of these plant groups in Upper Pennsylvanian coal swamps may have been made possible because they were widely spread in many habitats of lowland regions. Thus complete extinction was unlikely. In general, the vegetation of Upper Pennsylvanian coal swamps was more heavily dominated by tree ferns than that of the surrounding mesic lowlands and clastic wetlands, where pteridosperms remained the dominant plants. The nearly complete elimination of lycopods may have occurred because they were ecologically centered in swamps and, with the nearly complete elimination of their adaptive zone, persistence was obviated. The only arborescent form to persist, *Sigillaria*, was centered in clastic-substrate areas. There were significant changes in the species composition of compression floras during the Upper Pennsylvanian as well (Gillespie and Pfefferkorn, 1979), implying that evolution was occurring in areas outside coal swamps. Considering the major extinctions of coal-swamp plants that had occurred, it is likely that the introduction of plants to the coal-swamp environments was common and may have changed markedly the species composition of all groups from that of the late Middle Pennsylvanian.

Cordaites and conifers began to appear in lowland assemblages in significant numbers during the Upper Pennsylvanain. They attained dominance only in some limnic coal swamps of western Europe (Galtier and Phillips, 1979). However, the presence of significant amounts of *Lycospora* in these limnic coal basins indicates that some arborescent lycopods continued to exist in Stephanian coal swamps, even after they became extinct in the midcontinent. Eventually, coal-swamp floras were composed mostly of tree ferns and pteridosperms and surrounded by a lowland vegetation dominated by coniferophytic gymnosperms, creating an extreme in terrestrial island refugia (Galtier and Phillips, 1979).

Conclusions

The in situ evolutionary component of coal-swamp vegetational change is very difficult to distinguish from the effects of introduction and/or increasing abundance of taxa that were centered in neighboring mesic lowland environments. Without a detailed understanding of the ecological distribution of a plant group during the Pennsylvanian Period, it will be difficult to discern the degree to which the coal-swamp record reflects the general direction of evolutionary change in that group. It appears that once a species was introduced and became abundant in the coal swamps it underwent little morphological change and gave rise to few other successful coal-swamp species. This supports the concept of coal swamps as "closed systems," environments that for much of the Pennsylvanian may have been evolutionary refugia. The low levels of evolutionary change that we detect, and the concentration of vegetational change to periods of climatic transition, suggest that the refugial nature of coal swamps was a consequence of the stressful nature of the abiotic environment, which supported few species relative to the general lowland region. This may have resulted in a dynamic equilibrium within a coal swamp, in which randomly appearing patches due to disturbance were most likely to be colonized from within the edaphically closed ecosystem. It was only during times of swamp-community disruption, due to isolation of swamps from each other during times of stress, that forms newly evolved within the closed system could survive or that introduced species could establish.

What we presently know of coal-swamp and clastic-substrate vegetation suggests that they were markedly different. We should not expect these different kinds of environments to provide us with the same kind of information about evolution or to be accurate reflections of the nature or absolute number of speciation events that occurred in the other. The climatic change during the early Middle Pennyslvanian is recorded more clearly by the floral composition of coal swamps than by that of the compression floras because the swamps were a more uniform and vegetationally isolated kind of habitat. In contrast, the Upper Pennsylvanian swamps recorded only a calamity and not the later subtle changes that ultimately altered the vegetation in the surrounding lowlands. Clearly, the best evidence of climatic and evolutionary changes that occurred during the Pennsylvanian is to be obtained from combined coal-ball, palynological, and compression studies in the context of paleoecological interpretations gleaned from geologic and biological evidence.

Summary

Major changes in the vegetation of Pennsylvanian coal swamps are related to changes in climate. Two episodes of reduced moisture availability, one during the early Middle Pennsylvanian and the other, more severe, during the early Upper Pennsylvanian, produced the most extreme changes in the coal-swamp flora: (1) expansion of indigenous swamp plants to dominant levels within the swamps; (2) introduction or migration of plants into coal swamps from surrounding lowlands; (3) extinctions; and (4) evolution of new species that subsequently became prominent in coal-swamp environments. Of these, the evolutionary changes are the most difficult to document. The edaphic properties of peat substrates tended to isolate coal-swamp plants from the surrounding clastic-substrate vegetation, making coal swamps edaphic islands within the terrestrial lowland setting. The evolutionary fates of lineages centered in coal swamps were largely independent of the changes occurring in environments surrounding coal swamps.

Five major groups of plants comprised coal-swamp vegetation: lycopods, cordaites, ferns, pteridosperms, and sphenopsids. The lycopods, which were most abundant during the Lower and Middle Pennsylvanian, probably contributed the largest number of endemic species. Cordaites were prominent only in somewhat drier or brackish coal swamps. Tree ferns and pteridosperms entered coal swamps during the first dry interval, expanded during the subsequent period of rising wetness — in the late Middle Pennsylvanian — then dominated the Upper Pennsylvanian swamps. Sphenopsids were of relatively minor importance in coal swamps. Evolution in all groups except the lycopods probably was centered in clastic-substrate lowlands or uplands; coal swamps preserve a fragmentary portion of the evolutionary history of the groups.

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